

DIVISION S-7—FOREST, RANGE, & WILDLAND SOILS

Seedling Root Growth as a Function of Soil Density and Water Content

C. M. Siegel-Issem,* J. A. Burger, R. F. Powers, F. Ponder, and S. C. Patterson

ABSTRACT

Compaction caused by some intensive forest management practices can reduce tree growth, but growth reduction is the result of complex interactions between soil properties and tree physiological processes, which may differ by species. We used a 7 by 7 factorial greenhouse experiment to create a matrix of bulk density (ρ_b) and volumetric water content (θ_v) to better understand soil compaction effects on seedling growth of: (i) ponderosa pine (*Pinus ponderosa* var. *ponderosa* Dougl. ex Laws) grown on Dome and Cohasset soils; (ii) shortleaf pine (*Pinus echinata* Mill.) on a Clarksville soil; and (iii) loblolly pine (*Pinus taeda* L.) on an Argent soil. Models of root length density (RLD) were developed using multiple regression. The general model of $RLD = b_0 + b_1\theta_v + b_2\rho_b + b_3\theta_v^2$ described rooting response for the Clarksville-shortleaf and Argent-loblolly soil-species combinations ($p = 0.005$). However, the ponderosa pine RLD response on Cohasset soil was linear and there was an interaction between θ_v and ρ_b in the Dome soil. Shoot mass of seedlings growing within the least limiting water range (LLWR) was greater than those growing outside the range for all soil-species combinations except the Argent-loblolly pine ($p = 0.05$). The loblolly pines had greater shoot mass at θ_v above the upper LLWR limits (aeration limiting). Least limiting water range has potential as a soil quality indicator, but seedling response was not always associated with LLWR. Root length density (RLD) response surface models in conjunction with seasonal site water data have potential for determining compaction-induced soil limitations for tree growth, but need to be field tested and calibrated for both soil and species.

INTENSIVE FOREST MANAGEMENT can compact soils, which can change the soil air-water balance and potential for root growth. Studies conducted throughout North America have shown that tree growth and forest productivity decrease due to compaction. For example, soil compaction in southwest Oregon reduced ponderosa pine (*Pinus ponderosa*) height and volume growth 17 and 48%, respectively, and the effect was still evident 17 yr later (Froehlich, 1979). Growth reductions in height, shoot weight, and root volume have also been observed for 1-yr-old loblolly pine in the southern USA, with some variation due to site type (Hatchell et al., 1970; Simmons and Ezell, 1982). Similar results were found for *Pinus*

contorta, which had root weight, shoot weight, and stem height declines ranging from 50 to 90% resulting from compaction of several different soil types (Corns, 1988).

Although reduced growth from compaction has been reported across many regions, the effect on individual tree growth parameters is variable, and overall growth response varies for different species and soil types. For example, shoot and root weight of *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco and *Pinus monticola* Dougl. ex D. Don seedlings were not affected by compaction after one growing season, but root volume was 41% less for the *P. menziesii* (Mirb.) Franco seedlings and seedling height was 6% greater for *P. monticola* ($p = 0.05$) (Page-Dumeroose et al., 1998). Corns (1988) reported that *P. contorta* root weight, shoot weight, stem diameter, and stem height declined due to compaction on all four soils tested, but *Picea glauca* growth on two of the soils did not decline or increased twofold. *P. contorta* shoot weight decreased 64% on a silty clay soil when ρ_b increased from 1.2 to 1.5 Mg m⁻³, while shoot weight decreased 86% on a clay loam soil compacted to 1.5 Mg m⁻³. Wasterlund (1985) also reported species differences with *Picea abies* growth being more impeded by compaction than *Pinus sylvestris* L. growth. On several California sites, Gomez et al. (2002) reported that compaction effects on 4-yr-old ponderosa pines varied with soil texture and soil water regime. Stem volume on compacted soils was less, the same, and higher on clayey, loamy, and sandy loam soils, respectively. Compaction also favored *Picea mariana* (Mill.) B. S. P. and *Pinus banksiana* Lamb. growth on coarse textured soils classified as humo-feric podzols in northwestern Quebec (Brais, 2001). Growth increases on these soils were linked to harvest traffic compaction causing a more favorable pore-size distribution, which improved the balance between aeration porosity and available water holding capacity, similar to the findings by Gomez et al. (2002).

The persistence of compaction effects from forest harvest operations on tree growth and soil properties varies over time for different sites and species. Two studies with similar experimental designs in coastal Washington and inland Oregon report these results (Miller et al., 1996; Heninger et al., 2002). Bulk density increases on skid trails ranged from 2 to 40% for different soil types and persisted 8 yr after the logging operation (Miller et al., 1996). However, the effect of compacted skid trail

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Abbreviations: LLWR, least limiting water range; LTSP, USDA Forest Service Long-Term Soil Productivity Study; NLWR, nonlimiting water range; OWC, optimum soil water content; RLD, root length density; SWRC, soil water retention curves; ρ_b , bulk density; θ_v , volumetric water content.

soil on tree height lasted only one to two seasons for *P. menziesii*, but persisted more than 2 yr for *Tsuga heterophylla* (Raf.) Sarg. in coastal Washington (Miller et al., 1996). In comparison, Heninger et al. (2002) reported that *P. menziesii* growing on skid trails had height growth reductions that persisted for 8 to 10 yr on inland Oregon sites where soil textures were finer and the climate was drier. After 10 yr, trees growing on skid trails were 10, 14, and 29% less in height, diameter, and volume, respectively.

Several researchers have developed models to elucidate the roles that key soil properties such as soil strength, water, and aeration and their interactions have on plant growth. Greacen and Sands (1980) developed a conceptual model, which shows that compaction increases soil bulk density, which modifies both soil strength and porosity. These factors are further moderated by water content, and their combined interactions influence root growth. The concept of the non-limiting water range (NLWR), introduced by Letey (1985), combined the effects of several soil properties critical to plant growth into a single variable. The NLWR was defined as the range in which water availability is non-limiting to plants, generally bounded by field capacity and wilting point. As bulk density increases, the NLWR becomes narrower, with mechanical resistance becoming limiting at the dry end and poor aeration becoming limiting at the wet end.

Childs et al. (1989) used soil density and porosity data from a compaction study by Reicosky et al. (1981) to develop a generalized model relating soil physical conditions to root growth similar to Letey's NLWR. They also hypothesized that ideal root growth conditions were diminished with increasing soil density due to excessive soil strength at low water contents or inadequate aeration under wet soil conditions. In their model, ideal growth is depicted within a "root growth window" bound by non-specified water contents.

Da Silva et al. (1994) furthered these conceptual ideas by evaluating the NLWR as an index of the structural quality of soil. They used the term LLWR to recognize that plant response occurs along a continuum of water contents rather than as a step function. The critical limits defining the LLWR were: (i) volumetric water content (θ_v) at field capacity and permanent wilting point (potentials of -0.01 and -1.5 MPa, respectively); (ii) air-filled porosity $<10\%$; and (iii) soil strength >2.0 MPa (da Silva et al., 1994). All of these conceptual models attempt to integrate various soil property effects that, alone, do not fully account for root growth in a given environment. In a management context, one would want to maintain or improve those soil conditions that created the largest NLWR, LLWR, or root growth window. However, we need to determine if generalized models adequately reflect growth potential or if soil- and species-specific models need to be developed.

For a given region, soil type, and tree species, forest productivity is a function of θ_v as it varies with climate across the growing season, and a function of the inter-related factors of ρ_b , soil strength, and porosity. Root growth has been found to be a more sensitive indicator

of soil disturbance than shoot growth (Singer, 1981; Heilman, 1981). Additionally, reductions in root growth occur long before extreme soil strength or moisture conditions are reached (Eavis, 1972; Voorhees et al., 1975; Russell, 1977; Simmons and Pope, 1987). Developing soil- and species-specific root growth responses for a range of soil water, aeration, and ρ_b conditions would be valuable for assessing potential productivity declines due to compaction.

The USDA Forest Service Long-Term Soil Productivity Study (LTSP), composed of large-scale field experiments located at sites across the USA, was developed to assess the effects of soil compaction and surface organic matter removal on site productivity across a range of forest sites (Powers et al., 1990). Similar projects on industry lands have also been developed. To better understand the management implications of compaction, we used soils and associated tree species from a spectrum of LTSP study sites to test the hypothesis that best growth would occur at low ρ_b and moderate θ_v , while as density increased, aeration would become limiting to growth on wetter soils, and soil strength would become limiting for dryer soils.

Our specific research objectives were to: (i) develop a response surface describing tree seedling root growth as a function of soil ρ_b and θ_v ; (ii) examine seedling growth using the LLWR; and (iii) based on our response surface models, determine if generalized models adequately reflect growth potential or if soil- and species-specific models are needed.

METHODS AND MATERIALS

Site and Soil Descriptions

The four soils chosen for this study, Dome, Cohasset, Clarksville, and Argent series (Table 1), represent contrasting forest soils from LTSP field sites across the USA. All four soils are of moderate to large extent in their region and are important for timber production. The Dome LTSP site is located on the Sierra National Forest, Madera County, California at an elevation of 1576 m. Cohasset soil was taken from the Blodgett Research Forest LTSP study site in El Dorado County, California, at an elevation of 1350 m. The Clarksville soil was collected from Carr Creek State Forest, Shannon County, Missouri. Argent soil was taken from a MeadWestvaco/Virginia Tech long-term productivity research site in Colleton County, South Carolina. Typical soil series and site characteristics are presented in Table 1.

Surface soil (0–20 cm) samples were collected, air dried, and sieved (2 mm) to obtain the fine-earth fraction. The 0- to 20-cm soil depth encompassed all or most of each soil's surface A horizon. Particle-size analysis was determined for each soil by organic matter oxidation (Gee and Bauder, 1986) and subsequent standard mechanical analysis (ASTM, 1972), wet-sieving, and sand fractionation (Table 1). Carbon and N were determined by using a vario MAX CNS analyzer (Elementar, Hanau, Germany) (Table 1). Organic matter was determined as the organic C content multiplied by 1.72 (Nelson and Sommers, 1982).

Experimental Design

A seven by seven factorial greenhouse experiment was performed to assess root growth as a function of ρ_b and θ_v . A series

Table 1. Classification and site and surface soil characteristics of four forest soils from across the USA used in this study.

Soil series	Taxonomic class	Great group	Parent material	Location/landform	Typical vegetation	Surface horizon texture	Surface organic matter	C N	
								%	
Dome	Coarse-loamy, mixed, superactive, mesic	Typic Dystroxepts	Granodiorite residuum	Sierra Nevada Mountains hillslopes	Sierra Nevada mixed-conifer	CoSL (66-22-12)†	6	3.36	0.14
Cohasset	Fine-loamy, mixed, superactive, mesic	Ultic Haploxeralfs	Andesitic mudflow residuum	Sierra Nevada Mountains hillslopes	Sierra Nevada mixed-conifer	CoSL (63-20-16)	9	5.07	0.21
Argent	Fine, mixed, active, thermic	Typic Endoaqualfs	Marine sediments	Southeast Coastal Plain	Loblolly pine-hardwoods	FSL (65-20-15)	5	2.66	0.16
Clarksville	Loamy-skeletal, siliceous, semiactive, mesic	Typic Paleudults	Dolomite, Chert and sandstone residuum	Ozark Mountains hillslopes	Oak-hickory hardwoods	SiL (29-54-17)	4	2.29	0.12

† Percentage of sand-silt-clay is in parentheses.

of soil compaction tests determined the optimum technique for uniformly compacting soils in PVC cylinders that were used to assess compaction effects on various soil physical properties (Siegel-Issem, 2002). Polyvinyl chloride (PVC) cylinders with dimensions of 8 × 15 cm were packed at seven compaction levels with surface soil from each LTSP site. Compaction levels were assigned based on the range between the minimum and maximum ρ_b determined for each soil (Table 2). A gradient of seven levels of θ_v was established to cover the range from permanent wilting point to near-saturation for each soil (Table 2). Tree seedlings of species typically associated with each soil type were planted in the soil columns compacted at each of the seven ρ_b levels. Water contents at the seven different θ_v levels were maintained as closely as possible throughout the growing period. Approximately every 3 d during the growth period, all pots were weighed and watered as necessary to maintain the θ_v within a range of 10 to 15% of target θ_v . If weight was below target, water was added to achieve the target θ_v ; conversely, water was not added if the pot was too wet or within the range.

Soil Compaction and Bulk Density

Compaction testing equipment was manufactured specifically for this experiment to meet ASTM standards and allow us to use standard 8-cm PVC pipe as cylinders for creating compacted soil columns for soil analyses and planted seedlings (ASTM, 1996). A slide hammer was manufactured to meet weight specifications (2.5 kg) and slide smoothly in the PVC cylinder. Using a brace manufactured to secure the cylinder, the compaction hammer slid down a rod from a consistent height of 30.5 cm, allowing each hammer blow to evenly compact the soil layer in the PVC cylinder. Soil compaction standard effort tests on each soil were used to determine the optimum soil water contents (OWC) for compaction (ASTM, 1996). The OWC for each soil type was determined from graphs plotting soil water content as a function of soil ρ_b (Siegel-Issem, 2002). Subsequently, all soils were compacted at their OWC.

Compactive effort for each soil was determined as a variation of the ASTM compaction standard effort tests to assess differences in each soil's ρ_b range (ASTM, 1996). This procedure was used to determine the compactive effort (number of hammer blows) needed to achieve target ρ_b for the compacted soil columns used in subsequent analyses. Sieved and moistened soil was added to the PVC cylinder, the surface settled and smoothed, and then compacted in several lifts. Each lift of soil received a set number of blows (1, 2, 4, 8, 16,

32, or 64 blows) to relate a range of compaction hammer blows and ρ_b , similar to the work done by Howard et al. (1981). Soil volume, mass, and θ_v were measured and oven dry weight and ρ_b determined for each soil column. Minimum and maximum ρ_b for each soil were determined from graphs depicting ρ_b as a function of compactive effort, with maximum ρ_b being defined as the asymptote of the curve. Regression analyses on log transformed data were used to determine the relationship between number of hammer blows and ρ_b , and thus the number of compaction hammer blows needed to achieve each target ρ_b for the soil columns used in our experiment (Siegel-Issem, 2002).

Soil Strength

Soil strength was measured in each soil column at the end of the experiment with a lab pocket penetrometer (BSE Model

Table 2. Average bulk density and water contents of soil cores compacted at seven different target levels and maintained at seven water content levels in a 7 × 7 factorial arrangement.

Soil	Compaction level	Average bulk density	Water level	Average water content
		Mg m ⁻³		cm ³ cm ⁻³
Dome	1	1.04 ± 0.02	1	0.11 ± 0.03
	2	1.13 ± 0.01	2	0.13 ± 0.02
	3	1.26 ± 0.01	3	0.14 ± 0.02
	4	1.33 ± 0.01	4	0.18 ± 0.03
	5	1.42 ± 0.02	5	0.21 ± 0.04
	6	1.50 ± 0.01	6	0.27 ± 0.05
	7	1.54 ± 0.01	7	0.40 ± 0.09
Cohasset	1	0.81 ± 0.02	1	0.11 ± 0.00
	2	0.89 ± 0.02	2	0.17 ± 0.04
	3	0.96 ± 0.03	3	0.19 ± 0.04
	4	1.13 ± 0.00	4	0.24 ± 0.04
	5	1.19 ± 0.01	5	0.28 ± 0.05
	6	1.22 ± 0.01	6	0.34 ± 0.07
	7	1.26 ± 0.00	7	0.46 ± 0.11
Clarksville	1	1.13 ± 0.02	1	0.12 ± 0.02
	2	1.24 ± 0.02	2	0.14 ± 0.03
	3	1.29 ± 0.01	3	0.18 ± 0.04
	4	1.38 ± 0.01	4	0.23 ± 0.05
	5	1.45 ± 0.01	5	0.28 ± 0.06
	6	1.50 ± 0.01	6	0.34 ± 0.07
	7	1.53 ± 0.00	7	0.42 ± 0.12
Argent	1	1.27 ± 0.00	1	0.15 ± 0.04
	2	1.40 ± 0.01	2	0.22 ± 0.06
	3	1.48 ± 0.01	3	0.28 ± 0.08
	4	1.55 ± 0.01	4	0.33 ± 0.10
	5	1.61 ± 0.01	5	0.38 ± 0.13
	6	1.63 ± 0.00	6	0.44 ± 0.15
	7	1.65 ± 0.02	7	0.51 ± 0.18

S-170, Durham Geo-Enterprises, Stone Mountain, GA). All soil columns were near their targeted θ_v when measured. The column was placed on its side and the outer PVC cylinder cut lengthwise in several places. The PVC segments were removed and triplicate soil strength measures taken. The flat-tipped pocket penetrometer was fitted with a smaller-than-standard tip to measure the high strengths of some soils. Volumetric water content was determined for each soil column at the time of measurement by measuring gravimetric water content and adjusting for soil bulk density.

Soil Porosity and Air–Water Balance

Soil water retention curves (SWRC) were developed for all compaction levels within each soil type. Soil θ_v at soil water potentials (Ψ_w) of -0.005 , -0.01 , -0.03 , -0.1 , and -1.5 MPa were determined for each soil using standard tension table and plate techniques (Klute, 1986). Compacted soil columns (7.7 by 10 cm) were used to determine Ψ_w for tensions up to -0.1 MPa, and 5 by 2.5 cm soil columns were used to determine θ_v at a Ψ_w of -1.5 MPa. Soil porosity at several key Ψ_w ranges for all four soils along their ρ_b gradient was calculated from the SWRC: aeration porosity (Ψ_w between 0.00 to -0.01 MPa), available water (Ψ_w between -0.01 and -1.5 MPa), and unavailable water (permanent wilting point) (Ψ_w less than -1.5 MPa).

Least Limiting Water Range

The LLWR, as used by da Silva and Kay (1997), was developed for each soil using our experimental data. The upper LLWR limit is the lesser θ_v of field capacity (θ_{FC}) or aeration porosity $<10\%$ (θ_{AP}), while the lower limit is the greater water content associated with either wilting point (θ_{WP}) or soil strength >2.0 MPa (θ_{SS}). Soil water retention curve data from each of the seven density levels were used to determine θ_{FC} and θ_{WP} critical limits. θ_{AP} was defined as total porosity minus 10%. The θ_{SS} limit was determined using Busscher's (1990) regression model as selected by da Silva and Kay (1997) describing the relationship of strength as a function of bulk density and water content:

$$\theta_{SS} = c\theta_v^d \rho_b^e \quad [1]$$

where c , d , and e are constants.

Seedling Establishment and Growth

A 1-cm diam. hole was drilled in the center of each packed soil column to within 3.5 cm of the bottom. At planting time, this hole was back-filled with washed silica construction sand. The sand channel allowed rooting during seedling establishment, which was important in the highly compacted soil columns. Furthermore, the sand channel allowed water access to the soil column center along its depth, resulting in a more uniform θ_v , and minimizing high surface density impact on water infiltration. The volume of this channel is 1% of the total soil column volume and, therefore, a small fraction of the volume roots would eventually utilize. A fine mesh plastic screen was attached to the bottom of each PVC cylinder to prevent the loss of soil and allow water drainage. Soil columns were placed on a metal mesh greenhouse bench throughout the experiment.

Ponderosa pine was grown on the Dome and Cohasset soils from California, shortleaf pine on the Clarksville soil, and loblolly pine on the Argent soil. Seed stock appropriate to the areas from which our soils were collected was used. Seeds were planted in trays in a potting soil and sand mixture and were set in the greenhouse to germinate and grow. After 28 d, the most vigorous seedlings of approximately equal size were

selected and planted in the center of each pot. Approximately 0.5 cm of washed silica sand was added to the top of the soil to prevent soil surface disturbance from the watering treatments and to prevent the sand-planting channel from clogging with soil. The seedlings were grown for 6 wk with regular watering and nutrition to establish root growth before applying water stress.

After the establishment period, seedlings were grown for the experimental period of approximately 13 wk. We allowed the shortleaf pines on Clarksville soil to grow an additional 8 wk because these seedlings were still very small and roots had not fully exploited the soil volume after 13 wk. The average weekly minimum temperature during the study period was 18°C and the average maximum temperature was 33°C. Humidity ranged from 50 to 93% with a weekly average of 56%. A commercial fertilizer (15-30-15) nutrient solution was foliar-applied periodically to provide adequate nutrition throughout the experiment. At each fertilizer application, each seedling received 4.5 mL of fertilizer solution containing 710 mg L⁻¹ N, 610 mg L⁻¹ P, 590 mg L⁻¹ K, 7 mg L⁻¹ Fe, 3 mg L⁻¹ Cu, 3 mg L⁻¹ Zn, 2 mg L⁻¹ Mn, 0.9 mg L⁻¹ B, and 0.02 mg L⁻¹ Mo.

All seedlings survived the establishment phase. However, after watering treatments were applied, there was significant ponderosa pine seedling mortality on the Dome and Cohasset soils. Several shortleaf pines on the Clarksville soil died. No loblolly pines growing on the Argent soil died.

Plant Analyses

After the growing period, seedling height, and root collar diameter were measured. Each core was then deconstructed and root systems separated from the soil by washing with water. Root length was determined for each seedling's entire root system using a computer imaging analyzer (Delta T, Delta T Devices, LTD, Cambridge, UK) and RLD (length of roots per volume of soil) was determined. Shoots and roots were oven dried at 70°C and both above and belowground biomass were measured.

Model Development and Statistics

Multiple regression techniques were used to model root growth as a function of ρ_b and θ_v . We hypothesized that root growth would increase linearly with decreasing ρ_b (Foil and Ralston, 1967; Heilman, 1981; Mitchell et al., 1982). Furthermore, we hypothesized that root growth would be less both at the wet and dry ends of the soil water spectrum, with optimum growth occurring at moderate θ_v . Therefore, we hypothesized that this relationship could be depicted mathematically as a quadratic function. The basic model

$$RLD = b_0 + b_1 \times \theta_v + b_2 \times \rho_b + b_3 \times \theta_v^2 \quad [2]$$

was fit to each soil–species combination. We also used regression analysis to test if there was an interaction between ρ_b and θ_v . Terms were then added or deleted, based on their significance in the model, to reflect the observed data for each soil. Regression diagnostics (Cook's D and leverage analysis) were used to examine the influence of outliers on the model shape. Plots of the residuals were evaluated to assess model fit. Seedling growth in and out of the LLWR was compared with a t test. All statistical analyses were performed using the SAS statistical software (SAS Institute, 1999).

RESULTS

Soil Strength and Soil Air–Water Balance

At θ_v below 0.25 cm³ cm⁻³, soil strength became excessive at higher ρ_b , often exceeding 2.0 MPa, for all soils

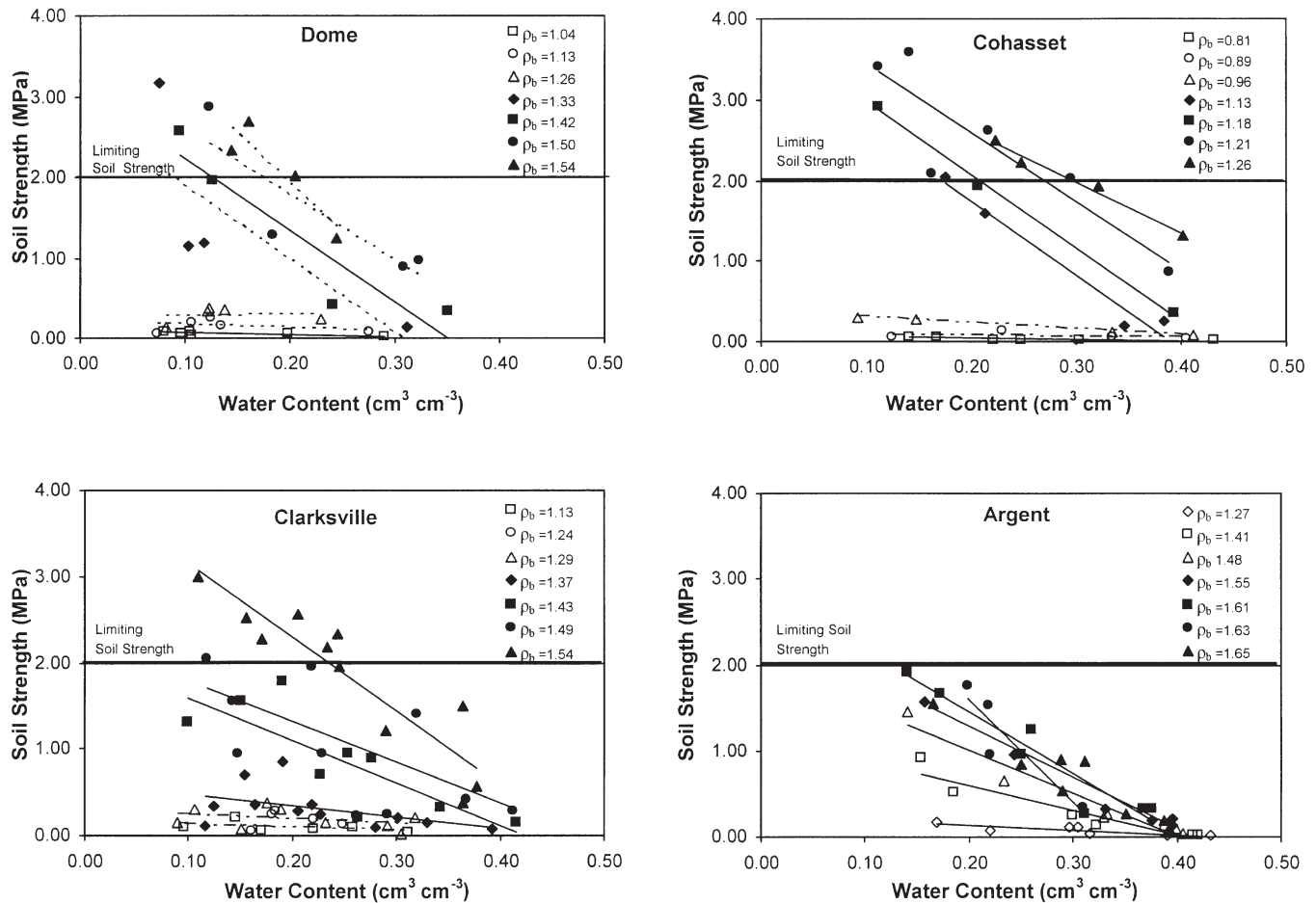


Fig. 1. Soil strength of compacted soil columns as a function of bulk density (Mg m^{-3}) and water content for four forest soils. Each point is the average of three strength measurements. Solid lines indicate that the linear relationship of soil strength as a function of volumetric water content for a particular bulk density level was significant ($P = 0.1$).

except the Argent soil (Fig. 1). However, the ρ_b at which soil strength increased significantly or exceeded 2.0 MPa was soil specific. The most compact and dry soil columns exceeded this limit at ρ_b above 1.13, 1.33, and 1.4 Mg m^{-3} for the Cohasset, Dome, and Clarksville soils. However, no Argent soil columns exceeded 2.0 MPa, but they did have the potential to exceed this value when ρ_b was above 1.55 Mg m^{-3} at θ_v dryer than we measured. At the lowest densities for all soils, strength was generally <0.05 MPa and not affected by θ_v .

Compaction increased ρ_b and reduced total and aeration porosity for all four soils (Fig. 2). The greatest total and aeration porosity reductions occurred for the Cohasset soil, which initially had the highest overall total porosity, available water, and aeration porosity of the four soils. At or above ρ_b of 1.13, 1.42, 1.44, and 1.55 Mg m^{-3} aeration porosity dropped below 10% for the Cohasset, Dome, Clarksville, and Argent, respectively (Fig. 2). Water contents above 0.35 $\text{cm}^3 \text{cm}^{-3}$, in combination with high ρ_b , created poorly aerated conditions, which limited root growth of shortleaf pines in Clarksville soil, and loblolly pines in Argent soil. For all soils, available water increased slightly with increasing compaction.

Least Limiting Water Range

We compared RLD of seedlings grown in and out of the LLWR (Fig. 3; Table 3). Root length density of ponderosa pine in Dome soil and shortleaf pine in Clarksville soil, growing within the LLWR range, was twice that of those growing outside the range. The RLD of ponderosa pines grown within the LLWR on Cohasset soil was 43% greater ($p = 0.108$) (Table 3). There was no difference between RLD of loblolly pines grown in and out of the LLWR on Argent soil.

We tested the root growth–tree growth relationship depicted in Greacen's and Sands' (1980) model by also comparing seedling growth in and out of the LLWR range (Table 3). Measured shoot growth for the Dome-ponderosa pines, Cohasset-ponderosa pines and Clarksville-shortleaf pines responded as predicted within and without the LLWR. The ponderosa pines growing within the LLWR on both Dome and Cohasset soils had greater biomass than those growing out of the range (Table 3). The mean weight of Dome-ponderosa pine seedlings within the LLWR was 0.53 g, while those outside the range weighed 0.27 g. Cohasset-ponderosa pine seedlings growing within the range were also larger than those outside the range at 0.33 and 0.21 g, respectively,

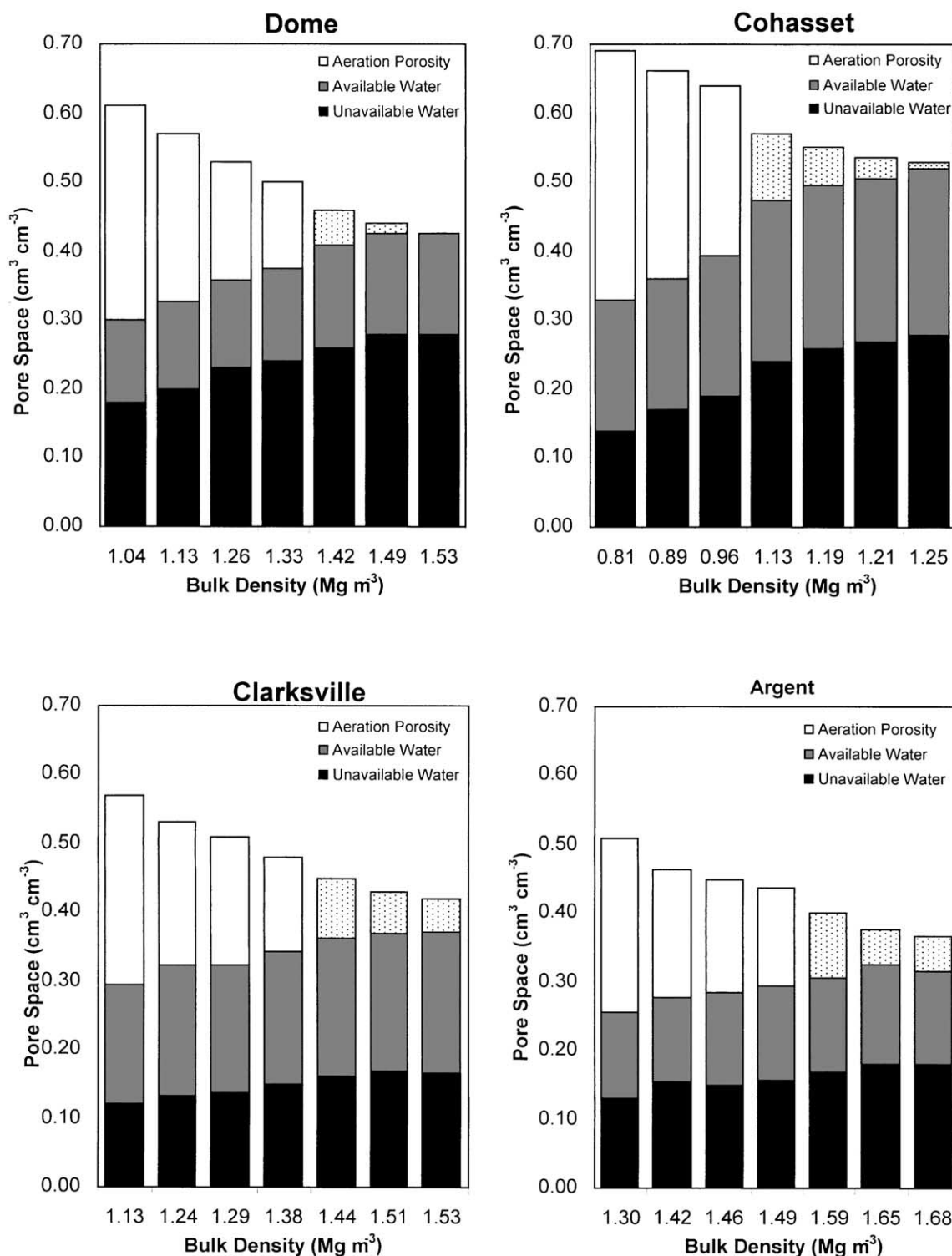


Fig. 2. Soil porosity changes resulting from compaction of four forest soils. Patterned aeration porosity bars denote aeration porosities <10%.

but seedlings within the range were slightly smaller than those on the Dome soil. Most ponderosa pine seedlings on Dome and Cohasset soils were limited by high soil strength and inadequate water based on the LLWR limits. However, ponderosa pine seedlings growing outside the aeration porosity limit on the Cohasset soil had greater root and shoot growth than trees growing within the LLWR at the same density. Mean shortleaf pine

shoot weight of trees growing within the LLWR range was twice that of those outside the range ($p = 0.009$) (Table 3). These seedlings were most limited by aeration and inadequate water.

The LLWR did not define loblolly pine growth on the Argent soil as predicted (Table 3; Fig. 3). The shoot weight of loblolly pine seedlings within the LLWR was less than those outside the range despite the fact that

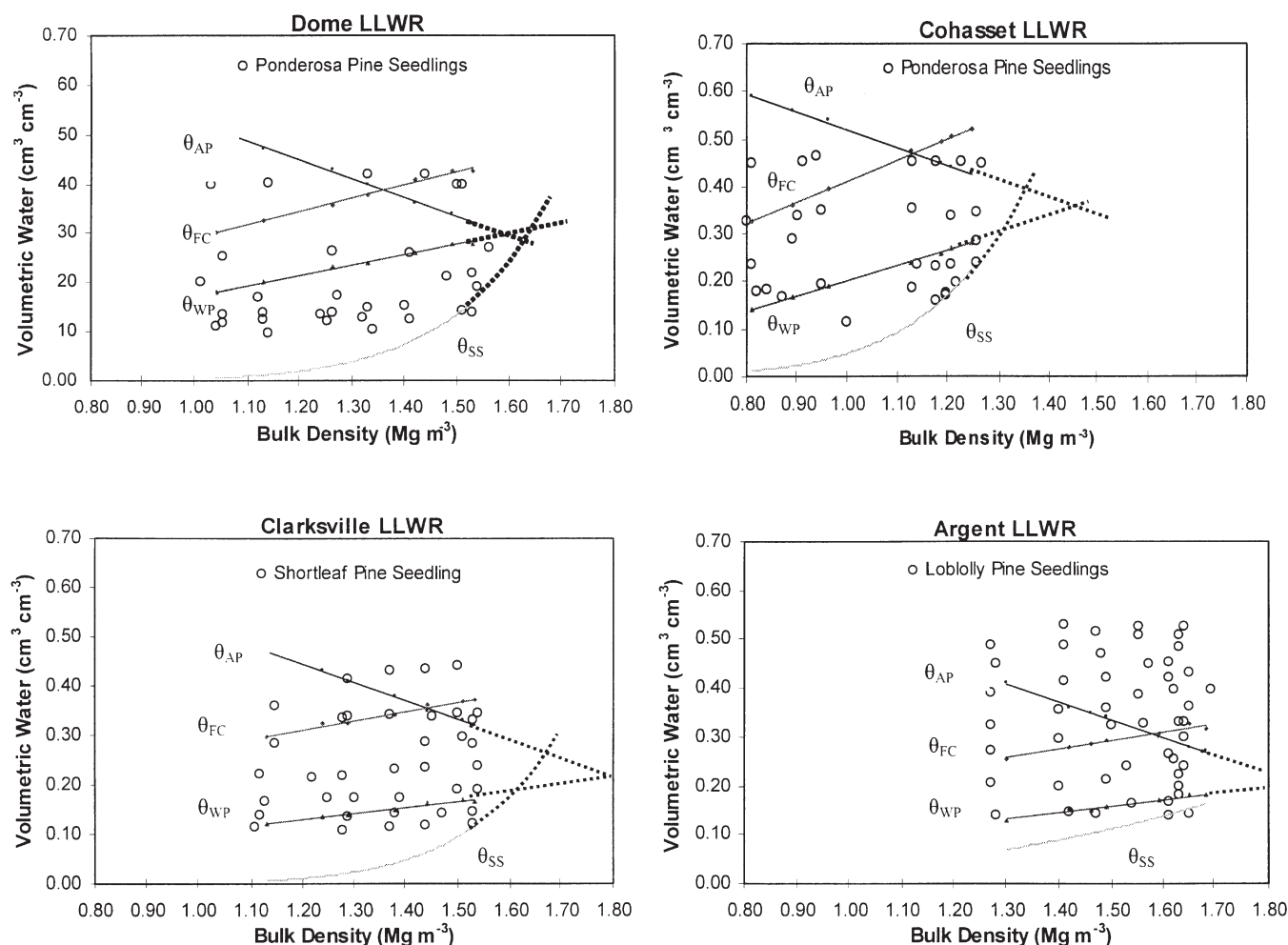


Fig. 3. Least limiting water range (LLWR) of several forest soils depicts the field capacity (θ_{FC}), wilting point (θ_{WP}), aeration porosity < 10% (θ_{AP}), and soil strength > 2.0 MPa (θ_{SS}) limit lines. Points on the graph represent seedlings grown at certain water contents and bulk densities. Dotted lines extrapolate limits beyond maximum soil bulk densities found in this study.

they grew at <10% aeration porosity. Mean shoot weight of seedlings growing within the LLWR was 0.44 g while it was 0.72 g for seedlings growing out of the LLWR. The LLWR underestimates the ability of loblolly pine to grow across a wide range of soil moisture conditions in the Argent soil. The LLWR did not correspond to the “best” growth of these seedlings; the θ_v contents associated with the standard limits are too low for the Argent soil growing loblolly pines.

Root Length Density Models

Root length density of shortleaf pine growing in the Clarksville soil and loblolly pine growing in the Argent soil responded to the soil water and ρ_b gradients as predicted (Fig. 4A,B). The RLD residuals plotted as a function of the predicted values for each soil were well distributed, indicating that there was no reason to believe that other terms would improve the model fit. Additional regression diagnostics determined that no individual points were outliers or had undue influence on the model shape. Together, θ_v and ρ_b had a significant effect on root growth, explaining 33 and 61% of the variation in RLD for the Clarksville and Argent soils,

respectively. The influences of ρ_b and θ_v on RLD were independent of each other. Root length density decreased linearly with increasing ρ_b and decreased as θ_v became wetter or dryer than 0.25 and 0.30 cm³ cm⁻³ for the Clarksville and Argent soils, respectively. Bulk density had a greater influence on shortleaf pine growing in Clarksville soil than loblolly pine in Argent soil. At higher ρ_b , the θ_v range in which growth occurred was narrower for the Clarksville-shortleaf pine than the Argent-loblolly pine; at a ρ_b of 1.6 Mg m⁻³, shortleaf pine roots grew within a θ_v range of 0.13 to 0.43 cm³ cm⁻³, while loblolly pine grew between 0.15 and 0.58 cm³ cm⁻³. Best growth occurred when θ_v was near 0.25 cm³ cm⁻³ for the Clarksville-shortleaf and between 0.30 and 0.35 cm³ cm⁻³ for the Argent soil (Fig. 4A,B).

Root length density of ponderosa pines growing on the Dome soil did not fit the general model (Fig. 4C). There was a significant interaction between θ_v and ρ_b ; therefore, the interaction term $\theta_v \times \rho_b$ was added to the general model. With the expanded model, ρ_b and θ_v explained 81% of the variation in RLD for the Dome soil. Root length density decreased with increasing ρ_b ; however, that effect was moderated by θ_v . The signifi-

Table 3. Mean root length density and shoot weight of tree seedlings growing in and out of the least limiting water range (LLWR) of four forest soils.

			Mean root length density			Mean shoot weight		
Soil	Tree species	Number trees†	In LLWR‡	Out LLWR	P value	In LLWR‡	Out LLWR‡	P value
			cm cm ⁻³			g		
Dome	ponderosa pine	4/27	0.28 (0.07)	0.14 (0.02)	0.029	0.526 (0.089)	0.267 (0.032)	0.008
Cohasset	ponderosa pine	17/14	0.20 (0.02)	0.14 (0.03)	0.108	0.326 (0.036)	0.208 (0.033)	0.025
Clarksville	shortleaf pine	21/17	0.23 (0.03)	0.11 (0.02)	0.003	0.493 (0.091)	0.218 (0.033)	0.009
Argent	loblolly pine	14/35	0.14 (0.02)	0.13 (0.01)	0.812	0.441 (0.056)	0.721 (0.066)	0.002

† Data stated as In/Out.

‡ Standard errors are reported in parentheses.

cant interaction of θ_v and ρ_b had the effect of lowering the θ_v at which best growth occurred as ρ_b increased, while decreasing growth to a greater extent on the wet end of the water gradient. Predicted best RLD of ponderosa pine on the Dome occurred in the θ_v range of 0.25 to 0.35 cm³ cm⁻³.

In contrast, the θ_v^2 term was not significant for the Cohasset-ponderosa pine; the RLD response surface was planar (Fig. 4D). Bulk density and θ_v had a significant effect on RLD and explained 77% of the variation in RLD. As ρ_b increased, RLD decreased. However, increasing θ_v improved growth along the ρ_b gradient.

DISCUSSION

For all four forest soil-tree species combinations, root growth decreased with compaction, and the magnitude of the effect was moderated by θ_v . The best growth occurred across a broader range of θ_v when the ρ_b was low. As density increased, θ_v at either the dry or wet end of the spectrum interacted with ρ_b to create either high soil strength or poorly aerated conditions, thereby diminishing the range in which normal growth occurred. The general regression model describing RLD as a linear function of ρ_b and quadratic function of θ_v was significant for two of the four soil-species combination and explained much of the variation in RLD. It is clear that root growth response is soil and species specific.

Although we cannot differentiate the exact causes of root growth limitations, it appears that soil strength and poor aeration, and combinations thereof are the primary causes of growth limitations at high ρ_b . Soil strength in excess of 2.0 MPa can significantly limit growth (Atwell, 1993; Greacen and Sands, 1980). An aeration porosity of 10% is often considered a critical limit for growth (Grable and Siemer, 1968). Eavis (1972) attempted to separate the effects of soil aeration, soil strength, and moisture stress on pea seedling growth and found that, generally, soil strength affected root growth in the Ψ_w range of -0.01 to -0.1 MPa, and water stress was the main factor at Ψ_w greater than -0.35 MPa. Voorhees et al. (1975) found that between Ψ_w of -0.01 to -0.1 MPa, pea seedling root elongation was more sensitive to aeration when soil strength was low and that RLD increased with increasing strength. Our data generally agree with these findings. At the dry end of the water spectrum, when Ψ_w was between -0.01 and -1.5 MPa, all soils except Argent, had soil strengths >2.0 MPa. At low ρ_b , inadequate water and poor aeration were the most likely cause of growth limitations. Furthermore,

poorly aerated soils can cause physiological imbalances that lead to nutrient deficiencies. Although we fertilized our seedlings throughout the experiment, many seedlings grown at the highest water/highest densities were chlorotic, suggesting nutrient deficiencies. Nitrogen and other minerals were deficient in shoots of *Pinus contorta* growing in compacted, remolded soil cores (Conlin and ven den Driessche, 1996).

The four soils used in this study were formed from various parent materials and had different organic matter contents. Three of the soils had sandy loam textures (Dome, Cohasset, and Argent), yet the combination of various soil physical properties caused each to respond differently to compaction. For example, at similar water contents, soil strength values were as high as 3.5 MPa for the Cohasset soil at a ρ_b of 1.21 Mg m⁻³, while the Argent soil never exceeded 2.0 MPa even at ρ_b as high as 1.61 Mg m⁻³. These soil differences created water and air dynamics variations which subsequently affected seedling growth response.

The LLWR is being used as an indicator to assess soil physical quality for a range of agricultural and forest soils (da Silva and Kay, 1996; Tormena et al., 1999; Betz et al., 1998; Zou et al., 2000). It can also be used to determine the amount of time that seasonal soil water conditions are ideal for growth. Da Silva and Kay (1996) found a strong correlation between corn shoot growth and the percentage of time θ_v fell outside the LLWR. Kelting (1999) determined the percentage of time that predicted daily θ_v were within the LLWR for a southeastern loblolly plantation but did not relate that directly to plant growth responses. We found significant differences for several growth responses of tree seedlings growing within the LLWR and those growing outside the range, but the results varied with parameter measured and species. Based on our results, the LLWR was not applicable for loblolly pine on Argent soil without modification. Nonetheless, the LLWR has good potential for evaluating soil quality, and in conjunction with species-specific growth models, may help predict potential productivity declines due to forest management impacts.

Compaction and low and high θ_v explained the least RLD variation for the Clarksville-shortleaf pine, compared with the other soil-species combinations. Root and shoot growth variability was high. Although there were up to 33% decreases in growth due to compaction they were not statistically significant. Shortleaf pine is a species that is found across a broad range of sites

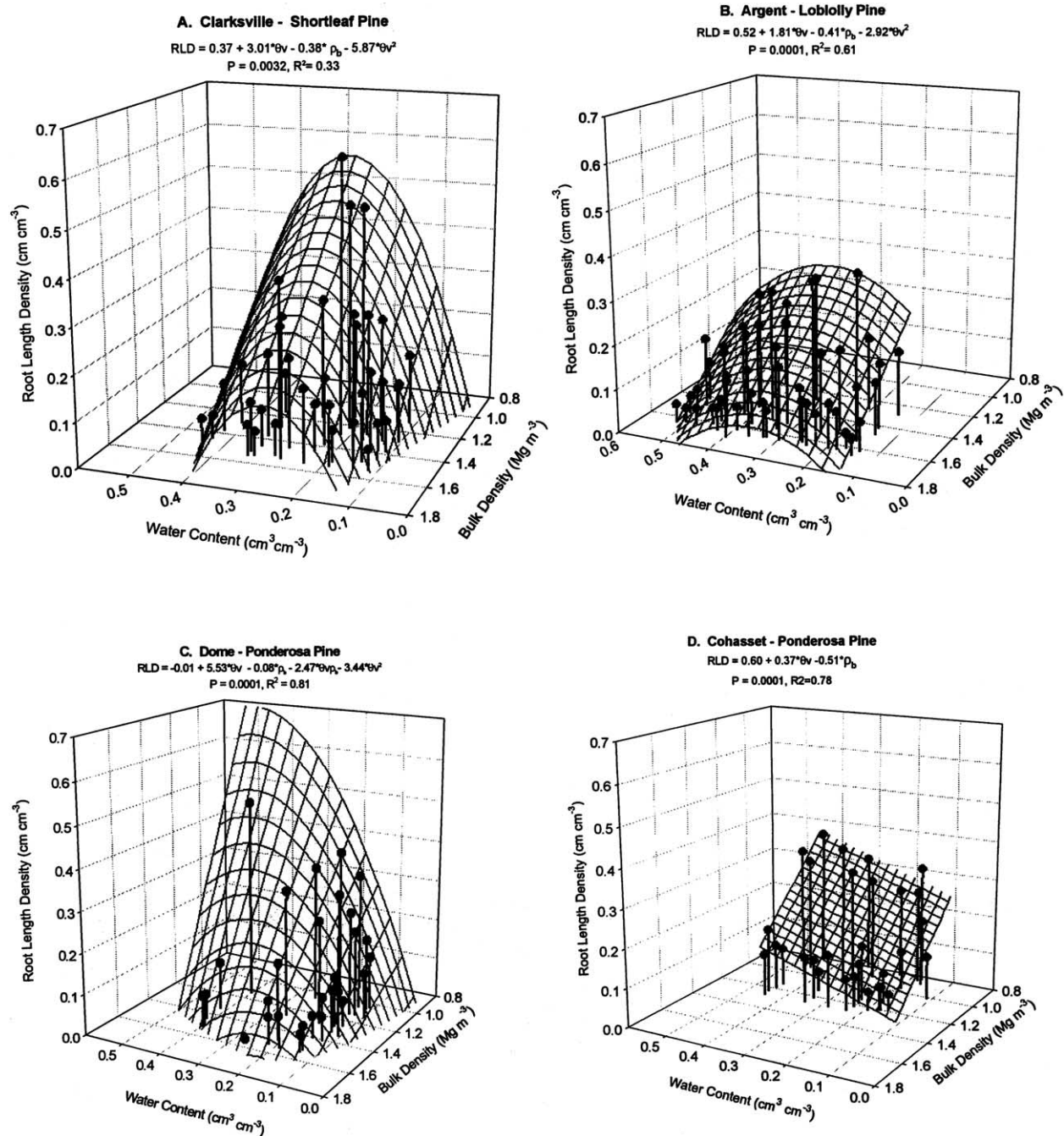


Fig. 4. Root length density of shortleaf pine seedlings, loblolly pine seedlings, and ponderosa pine seedlings grown on (A) Clarksville, (B) Argent, (C) Dome, and (D) Cohasset soils, respectively, as a function of soil bulk density and water content.

due to its tolerance for a wide range in soil conditions; however it does best on soils with silt loam and fine sandy loam textures (Lawson, 1992). Our soil, also a silt loam, had a wide LLWR allowing for less limited growth of this adaptable species across a wider range of water contents.

The Argent-loblolly pine combination appears to be the least affected by compaction and poor aeration of the four soil-species combinations we tested due to a combination of Argent soil properties and loblolly pine species adaptations. Increasing soil density decreased growth; however, the θ_v had much less influence on

loblolly pine RLD. The Argent soil, a fine sandy loam, had relatively low soil strengths, even at high ρ_b . We attribute this to the nature of the rounded, fine sand particles we observed and the clay mineralogy causing low shear strength. Low friction of these rounded, uniform particles, combined with the clay fraction's ability to hold water, probably allowed roots to move more easily through the soil. Furthermore, loblolly pines are adapted to poorly aerated soils and can tolerate occasional flooding with root anatomy changes that allow O_2 to diffuse from the stem to the roots (Schultz, 1997). These changes include development of aerenchyma cells

and intercellular spaces and formation of lenticels around the root collar (McKevlin et al., 1987; Topa and McCleod, 1986).

Ponderosa pine growth decreased with increasing ρ_b on the Dome soil and was affected by inadequate aeration porosity when ρ_b were above 1.42 Mg m^{-3} and θ_v were above $0.30 \text{ cm}^3 \text{ cm}^{-3}$. The seedlings in these pots were much smaller and were chlorotic for most of the growth period. This soil and species are from a Mediterranean climate with little rainfall and rapidly draining soil; therefore, inadequate soil aeration would seldom be a problem. The very dry conditions normally encountered, and subsequent increases in soil strength, could be detrimental to growth. Gomez et al. (2002) found enhanced ponderosa pine volume growth due to compaction on a similar sandy loam soil. On their site, ρ_b increased from 1.13 to 1.33 Mg m^{-3} in the top 30 cm and the resulting porosity change effectively increased available water by up to 10% on this typically droughty site. The non-compacted and compacted densities they found are comparable to the densities we created in our soil columns; however, we did not find the same growth increases with compaction. We attempted to maintain our soils at consistent θ_v and so the benefit of increased available water holding capacity was not evident.

Inadequate water and high soil strength appeared to be the prime factors causing poor ponderosa pine growth and high seedling mortality on the Cohasset soil. Fifty percent of the trees that died were from the two lowest water levels. Even though aeration porosity was less than 10% when ρ_b exceeded 1.13 Mg m^{-3} , infiltration and drainage were fairly rapid for this soil throughout the density range; therefore, we were not able to maintain near-saturated conditions over time that might have led to limiting aeration. Of the seedlings growing under the wettest conditions, we did not observe any hypoxic characteristics such as the chlorosis noted on the Dome-ponderosa pine seedlings. Aeration limitations due to low macroporosity from compaction may not occur for soils that are rarely saturated (Aust et al., 1998).

A discontinuity in RLD of ponderosa pines growing on Cohasset soil that corresponded with a sharp increase in soil strength was evident above a ρ_b of 1.0 Mg m^{-3} . Root growth decreased dramatically at the higher ρ_b . This is interesting given that we would generally consider this to be a low or even ideal ρ_b . However, for this soil, this density was very compacted. Forest soils such as Cohasset, with high organic matter contents, high porosities and andic properties, may be very compact even at low densities (Howard et al., 1981; Gomez et al., 2002).

In contrast, Gomez et al. (2002) found no stem volume differences for 5-yr-old ponderosa pines growing on compacted Cohasset soil from the same LTSP site from which we collected our loose Cohasset soil. The compacted field density they measured, 0.95 Mg m^{-3} , falls below the threshold ρ_b at which we found large soil strength increases. In fact, aeration porosity at that ρ_b exceeds $0.2 \text{ cm}^3 \text{ cm}^{-3}$ and available water is not affected (Fig. 2). Compared with a clay and sandy loam soil, the loam Cohasset soil had the greatest increases in soil

strength due to compaction, a finding similar to our strength results on compacted soil columns. Based on the LLWR we determined for this soil and data collected periodically from May to September by Gomez et al. (2002), the Cohasset LTSP site was within the LLWR during this period. Although we show that growth reductions due to poor aeration or high strength are possible for this soil, if moderate θ_v contents are present during most of the growing season, these factors will have little effect on growth.

The applicability of studies conducted under greenhouse conditions is limited without field validation. Conditions that exist in the greenhouse soil column are not often found in the field. Forest soils have much greater spatial and temporal heterogeneity due to the actions of rocks, roots, animals, and climate in modifying the rooting environment. However, data published by Gomez et al. (2002) presented a chance to compare lab and field results for two of our soils. Their Blodgett site is the same California LTSP field site from which our Cohasset soil was taken, while their Rogers site is the Chaix soil series—a different series than our Dome, but formed from the same parent material and taxonomically very similar (coarse-loamy, mixed, superactive, mesic Typic Dystroxerepts). We used the ρ_b 's Gomez et al. (2002) reported for the control and compacted field plots, their θ_v for spring (May) and summer (July) 1999 field measurements ($0\text{--}15 \text{ cm}$), and their stem volume increments for ponderosa pine in that year. We applied equations in Fig. 4 to their soil data to estimate RLD for their two sites and converted these to potential shoot weights from linear functions correlating shoot growth with root growth. Predicted shoot weights were transformed to relative shoot growth by setting growth for the control treatment to 1.00 (Table 4). Similarly, stem volumes measured in the field also were transformed to relative stem growth in 1999. Predicted relative growth from our models was compared against measured relative growth in the field.

Our RLD models accurately predicted the direction (+ or −) of stem growth in the field (Table 4). Our model also estimated the magnitude of field response to compaction with on the Cohasset soil. For the Chaix soil, our model underestimated measured field growth based on May field θ_v and overestimated field growth based on July θ_v . This indicates that our model has potential for predicting growth in a field setting but further calibration is needed. Using integrated seasonal volumetric water content with the growth models, rather than point-in-time samples, would better test the models and their ability to predict growth.

Our models are the first step in the process of determining the potential root growth for trees growing in these soils. Root growth under various field and management conditions could be estimated by dynamically applying seasonal water content variations in conjunction with seasonal rooting patterns and the proportion of time that ideal water contents for growth are present. Spatial heterogeneity of field ρ_b and subsequent rooting patterns will also influence the ability of the model to predict productivity losses due to compaction. We used

Table 4. Effects of soil bulk density and volumetric water content on predicted (p) and measured (m) field responses of ponderosa pine on two California LTSP sites in spring and summer 1999. Relative growth expressed as annual increment in stem mass or volume (from Gomez et al. 2002).

Soil series and texture	Variable	May		July	
		Control	Compacted	Control	Compacted
Chaix fine sandy loam	P _b	1.13	1.28	1.13	1.28
	θ _v	0.18	0.29	0.04	0.20
	RLD _p	0.281	0.285	0.004	0.224
	Relative growth _p	1.00	1.01	1.00	4.48
	Relative growth _m	1.00	2.67	1.00	2.67
Cohasset loam	P _b	0.75	0.89	0.75	0.89
	θ _v	0.28	0.38	0.20	0.25
	RLD _p	0.321	0.290	0.292	0.239
	Relative growth _p	1.00	0.92	1.00	0.88
	Relative growth _m	1.00	0.94	1.00	0.94

soil from the top 20 cm of the profile, which is the depth at which most roots are found and where compaction is often the greatest (Kozlowski, 1999). However, rooting is not restricted to the top 20 cm of soil, and roots will preferentially use any channels created by old roots or soil biota, thus reducing effects of compaction. In a naturally regenerated stand of loblolly pine, root density was greater in decomposing root systems at depths > 20 cm than in the soil matrix (Van Lear et al., 2000). Nambiar and Sands (1992) found that roots proliferated in perforations simulating natural soil channels of subsoil compacted zones, mitigating the effects of compaction on tree growth. Determining the percentage of time soil moisture is adequate and the percentage of roots utilizing root channels versus bulk soil matrix would help improve applicability of our models for assessing management impacts on root growth opportunity.

CONCLUSIONS

In general, trees grown on soils with lower densities have better ability to grow well across a broader range of soil moisture conditions. Soil strength and aeration limited growth, but the effect was not consistent across all soil-species combinations. The generalized RLD model generally worked, but the modifications needed to achieve the best fit, show that response is both soil and species specific. We created LLWR and RLD models based on sieved, hand compacted surface soils. The uniformity of soil conditions and controlled watering in this greenhouse experiment allowed us to interpret soil physical property effects on growth. However, the final value of these models depends on their ability to predict growth response under field conditions, which can be highly variable. Using and testing these models with field compaction soil property changes, tree growth responses, and seasonal water conditions is the next step. Combining this information with other models such as the LLWR will enhance our ability to predict overall potential loss of productivity due to compaction for different soil-species combinations.

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